Gymnosporangium Juniperi-Virginianae

The Cedar Apple Rust

by

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Topical Outline

Appendices

GYMNOSPORANGIUM JUNIPERI-VIRGINIANAE

I. The Cedar Apple Rust

A. History

The name _Gymnosporangium juniperi-virginianae_ was first given by Schweinitz (1822, p.74) in 1822 when he described the organism on _Juniperus virginiana_. Link, in 1825, described the same species in the Species Plantarum as _Gymnosporangium macropus_ (1825, p.128) and this name persisted until about 1915. It seems likely that the confusion which arose from the Schweinitzian use of compound names and from the fact that _Juniperus virginiana_ is host to other species of _Gymnosporangium_ gave the resultant preference to the nomenclature adopted by Link. In fact, Schweinitz (1831, p.57) speaks of the organism as _Podisoma macropus_ in 1831 while Fries (1832, p.57) in 1832 adopted the name of _Podisoma juniperi-virginianae_. According to the rule of priority, however, the name given by Schweinitz in 1822 must be regarded as valid.

Oersted (1865, p.291) in Copenhagen first proved by the use of cultures in 1865 that _Gymnosporangium_ rusts were heteroecious, i.e., the telial stage on the _Juniperus virginiana_ and the aecial stage or _Roestelia_ on the leaves of apples were merely different stages in the life history of the same organism. Up to this time, the telial stage and

the aecial stage were not supposed to have any genetic connection. De Bary (1865, p.222) in Germany, Cornu (1875, p.121) in France, and Cramer (1876) in Switzerland later confirmed the conclusions of Oersted. Since that time all species of <u>Gymnosporangium</u> have been shown to have a Roestelia stage.

The repeated experiments made by Farlow (1880, 1881, 1885, 1886), Halsted (1886,1887, 1889, 1891), Sanford (1888), Galloway (1889), Jones (1890, 1891), Pammel (1891) and others, leave no doubt about the genetic connection between <u>Gymnosporangium juniperi-virginianae</u> and <u>Roestelia pyrata</u>.

In the eastern part of the United States the need for protection from the ravages of the disease became apparent to many pathologists almost simultaneously.

Galloway of the United States Department of Agriculture reported in 1889 on experimental spraying in Vineland, New Jersey. In the same year, Halsted discussed the possibility of differing susceptibilities of various apple varieties. Jones, working in Vermont in 1890, used an ammoniacal copper carbonate spray on infected apple trees, reporting the results two years later. In Iowa in 1891, Pammel sprayed several wild crab apple trees for the purpose of seeing whether this fungus might be controlled by spraying but found there was little benefit derived from the practice. There was but little apple rust in Iowa at this time.

Thaxter made the first recommendation to control apple rust by eliminating cedar trees in 1891. He recommended that

the adjacent cedars be cut down, although he admitted that the virulence of the disease is, of course, proportionate to the proximity of the cedars. Following this, Jones, in 1891, reported wonderful success after removing all cedar trees within a one mile radius around an apple orchard that had been previously badly infected. By 1901, the South must have been rather generally suffering from the disease because Austin reported several spraying experiments in Alabama. After 1900, the literature on apple rust became more common as the economic importance of the fungus made itself felt in the leading apple-growing states.

In 1903, it was reported that the disease affected apples in Wisconsin, Nebraska, Minnesota and Iowa. The fungus had been recognized for some time, however, on its other hosts in those states. Pammel wrote in 1905 that a severe infection had been experienced in Iowa and nearby territory during the summer of 1904. The Nebraska Agricultural Experiment Station carried out successful experiments the following year, Emerson reported. In 1906, Heald initiated an intensive study of the whole problem in the same state, especially emphasizing the life history of the causal fungus and the possibility of controlling the infection on the alternate host, the red cedar. In 1908, Hein reported on strains of apples resistant to infection by the rust. At the same time, R. E. Stone reported on cedar apples and leaf rust in Alabama.

Between 1910 and 1920, Stewart and Kern made a special study of apple rust in New York and pointed out the importance of cultures in establishing the host relationships of species withinthe genus. Farlow, however, in 1885 had pioneered in this field. Other studies were made by Jones and Bartholomew in Wisconsin (1911-1915); by G. E. Stone in Massachusetts (1911); by Clinton and Britton in Connecticut (1911); by Lloyd and Ridgeway in Alabama (1911); by Coon in Nebraska (1912); by Giddings and Neal in West Virginia (1913); by Giddings in West Virginia (1913); by Fulton in North Carolina (1913); by Giddings and Berg in West Virginia (1914); by Fromme in Virginia (1914); by Reed, Cooley and Crabill in Virginia (1914); by Reed and Crabill (1915); by Weimer in New York (1917); by Crowell in Massachusetts in 1934 and MacLachlan in 1935; by Crowell and MacLachlan in Massachusetts in 1937; by Hamilton in New York (1937) and others. The amount of work done in this field and the amount of literature written on the subject may be taken as indicative of the economic importance of apple rust as a plant disease.

B. Hosts

All species of Gymnosporangium, except one, in which all four forms of spores are unknown, require two host plants for their complete development, i.e., are heteroecious. The species under study requires the Red Cedar, <u>Juniperus virginiana</u>, for one cycle of development and a pomaceous

plant for the other. The pomaceous plants thus far listed as hosts are the cultivated apple (Pyrus malus), the wild crab-apples (Pyrus angustifolia, P. coronaria, P. ionensis and P. baccata). The red cedar serves as a host during the development of the telial and sporidial stages; the pomaceous tree during the spermatial and aecial stages. The stage of the fungus on the red cedar was known for many years before proof was afforded that it was one stage in the development of the Roestelia or "cluster-cup" on the leaves of the pomaceous trees. Farlow obtained incomplete proof of the identity of the two fungi in 1877. The identity of the two was fully proved by Thaxter in 1887. Prior to this time, the stage of the fungus found on pomaceous trees was known as Roestelia pyrata (Aecidium pyratum by Schweinitz), but Thaxter proved that this stage could only be produced by sowing the sporidia of the Gymnosporangium from the cedar trees upon the foliage of the pome.

C. Cause

Cedar rust is caused by one of the true rust fungi, Gymnosporangium juniperi-virginianae Schw., an heteroecious pathogene, which passes a portion of its life cycle on the apple tree and a portion on the common red cedar, Juniperus virginiana. It is necessary for the perpetuation of the disease that the two hosts be near each other. The original

observers of the stages on the two hosts thought they were individual fungi, but Oersted established that they were identical.

D. Common Names

Gymnosporangium juniperi-virginianae is known most commonly as cedar rust. Apple rust is the name commonly applied to the aecial stage. The galls are known as cedar apples or cedar flowers. Other names used to designate this disease are leaf rust, rust of apple, cedar apple rust, cedar rust disease of apples, stem rust, fruit rust and orchard rust.

E. Life History

In the spring, horns or telial sori emerge from the galls on the cedar trees. Warm spring rains cause the telial sori to gelatinize and expand tremendously. Teliospores embedded in the horns germinate and produce promycelia with secondary spores or sporidia. As the rains cease and the humidity drops, the sporidia are dispersed by the wind. If they fall upon leaves of the proper age and of a susceptible variety of apple, infection of the leaf begins. The first symptom of infection manifests itself on the dorsal aspect of the leaf. These lesions or pycnia are followed later by aecia or cluster cups on the under side of the leaf. Aeciospores are formed within the cluster cups. When the spores mature, the aecia rupture,

assuming a stellate appearance as the strands recurve from the center. The aeciospores are carried by the wind to the red cedar. It is not understood if germination begins immediately or the spores overwinter on the cedar. When infection starts, the cedar hypertrophies at that point producing the typical "cedar apple". The gall reaches maturity in the late fall and is ready to begin the cycle again in the spring.

F. Symptoms

1. Cedar

The disease appears in the red cedar in the form of galls which increase gradually in size until they reach a diameter of nearly two inches. The color of the young minute gall is first green but it gradually becomes brown as maturity nears. Many black brittle-appearing galls or cedar apples are observed on trees bearing both the immature green galls and the mature chocolate-brown reniform apples. These are for the most part dead galls which are no longer capable of spore formation. Such galls often remain on the tree for a year or longer.

In June, the young galls may be first observed as tiny green outgrowths in the axils of the leaves of the red cedar. The growth of galls is rapid during the months of July, August and September. By November, the gall has reached its mature

size and form. Over the globular, sub-globular or reniform surface of the gall, rounded depressions become evident. The number of depressions is usually in direct relation to the size of the gall. In the following spring, gelatinous horns called telia are projected through the corky gall wall at the site of the depressions. The telia which are cylindric-acuminate in shape and orange in color, vary in length according to factors of gall size, temperature and amount of humidity.

The number of horns varies from one to several hundred. Heald in 1909 in Nebraska found that trees between 20 and 30 years of age were most infected and seemed to suffer the greatest injury from infestation. A large tree heavily infested in the spring appears to be "in flower". For this reason, the gall with its protruding horns at this stage is commonly referred to as a "cedar flower".

"The teliospores are oval to acuminate, frequently constricted at the cross septum and 15 to 20 by 46 to 60μ. With the absorption of water from the spring rains, the sori swell to enormous size and become more gelatinous. The teliospores germinate _in situ_. This may be repeated during periods of rainy weather, up until about June 1.. There may be one to as many as six or even more periods of telial germination before the supply is exhausted, the number of periods depending upon the weather conditions. Each cell of a teliospore can grow out into an hypha-like structure, the

promycelium, which under typical conditions becomes four septate. There is left, therefore, a sterile stalk cell and four fertile or basidial cells, each of which produces a secondary spore borne on a short lateral projection, the sterigma. A teliospore thus produces eight sporidia." (Heald, 1933).

A typical red cedar infested with galls and examined during the summer will commonly have three types of galls; young developing green galls, galls which may bear the shriveled remains of telia from the spring sporulation and black dried galls which have persisted from previous years.

Some cedar trees are very heavily infected while others seem to suffer little from the disease. In the states where the cedar tree is highly prized for its values as an ornamental plant or as a windbreak, some attention has been paid to the disease on the cedar tree. Spraying has been advised by some investigators to prevent death of the tree under such conditions but the results have not been good.

"It has been estimated that a single gall $1\frac{3}{4}$ inches in diameter may produce the enormous total of 7,440,000,000 sporidia which may emphasize the fact that a single cedar tree may be a menace to an entire orchard." (Lloyd and Ridgeway, 1911, p.3)

2. Apple

The leaves and fruits of susceptible apple trees are

affected by the rust as also, in a lesser degree, are the tender young twigs. In the territory where the disease is common, leaf attacks are rife and in some localities, are the chief phase of the trouble.

About ten days after the "cedar apples" on near-by cedar trees have become gelatinous, the first rust appears on the upper surface of the apple leaves as tiny spots about one-half millimeter in diameter and greenish yellow in color. Gradually these spots grow larger and deepen in color until they are orange, sometimes with reddish edges. In the center of the spots, diminutive pustules, pycnia, appear, gradually showing as minute black specks. Soon, the leaf tissue under the spots begins to hypertrophy, especially if the spots are distinctly separate, and produces a cushion or blister, $\frac{1}{4}$ to $\frac{1}{2}$ inch in diameter. Miniature tube-like projections called "cluster cups" or aecia appear on these blisters and when they mature in late June or July, burst open to assume a stellate form. At the base of each open cup is a mass of brown powdery spores.

This is the typical procedure in leaf infections but sometimes variations occur. If susceptible varieties have too numerous infections or resistant varieties have aborted infections, differences may be noted. Should the leaves be heavily infected, some susceptible varieties growing near cedar trees having 200-300 per leaf, the spots remain fine and coalesce. In some instances, the leaves yellow and drop off

or curl up before the aecia are formed. Occasionally, circular brown spots of dead tissue about one-eighth inch in diameter showing tiny black pustules in the center are formed. Since the central pycnia resemble pycnidia, these infections may be due to imperfect fungi. Too, some rust spots do not develop all summer, seeming unable to form the pycnia. These aborted infections are discovered either on resistant varieties or susceptible varieties which have escaped infection until the leaves have almost matured.

The current year's growth of twigs of extremely susceptible varieties may also be infected but not as generally as leaves and fruit. The affected twig increases in diameter not in length. Slightly enlarged blisters covered with the characteristic aecia may be found either at the nodes, surrounding and involving a bud or in internodal areas.

Young fruits of susceptible apple varieties may be thoroughly infected. Fruit lesions larger than others are the rule. The lesions may be localized at the calyx and involve the calyx lobes; they may be at the stem end; they may be on the side or generally over the entire fruit. New infections appear much as the upper surface lesions on leaves, but later cluster cups break through these lesions, usually appearing in a circle around the focal pycnial pustules. Frequently a greenish or yellowish discoloration extends to the core and pycniospores may be found in the core. Minor infections of the fruit merely spoil its appearance whereas more severe cases deform and atrophy it. As a rule, rust

spots do not increase either in size or number during storage.

The defoliation of apple trees resulting from leaf infections is most injurious to the trees. Susceptible varieties growing adjacent to cedars may have so many lesions on their foliage that it appears yellow. These trees drop their leaves early. Leaf fall has been proved proportional to the number of infections per leaf. Giddings and Berg report that in 1914, York Imperial leaves with ten or more rust lesions showed a dropping of 55% before September first. Since first the infection and then the resultant dropping of leaves severely drain the trees' vitality, they enter the winter rest in a weakened condition. Giddings even states his belief that leaf infection is much more important than fruit infection in determining the size of the ripe fruit. Severe leaf infections may even carry over their effect into the next year. Fewer lesions per leaf are necessary to defoliate the weakened trees the next year.

Reed and Crabill (1915, p.57) maintain that affected leaves seem to lose control of their transpiration, that photosynthesis in rusted leaves is greatly retarded, and that respiration is accelerated.

In recording aberrations, a further case shows that at times the leaf dies at the point of infection. A round area of dead tissue up to ½ inch in diameter is formed with a cluster of black pycnia at its center. These do not change further. Later in the season these dead patches may be

attacked by saprophytic fungi like Cladosporium or Alternaria. These would be difficult to identify if their development had not been watched.

G. Geographical Range

Gymnosporangium juniperi-virginianae is found only in North America. A careful examination of the literature fails to reveal its presence in any other part of the world. The fungus was known to plant pathologists for a long time, but it remained for Farlow in 1880 to forcibly direct attention to the organism. During the last thirty years, many investigations have been conducted bearing on the life-history of the organism and on the method of control of the disease. Consequently, the limits of the geographical distribution of the disease may be fixed fairly reliably by a plotting of the reports rendered to date. In general, the apple rust stage is widely distributed throughout the central and eastern half of the United States wherever the red cedar and apple occur together. Giddings (1918, p.8) reported an infection in Ontario, Canada and Alaska. The eastern boundary in this country is defined by Maine, Massachusetts, Rhode Island, New York, New Jersey, Delaware, District of Columbia, Maryland, Virginia, North Carolina, South Carolina, Georgia, and Florida. The southern limits are marked by Florida, Alabama, Mississippi, Louisiana and Oklahoma. The western limits are,

in general, marked by the eastern side of the Rocky Mountains. Rust on apple species has been reported from Oklahoma, Colorado, Nebraska and South Dakota. Those northern states which border on the Great Lakes set the northern limits. An alphabetical list of states which have reported cedar apple rust follows:

Alabama	Louisiana	Ohio
Arkansas	Maine	Oklahoma
Colorado	Massachusetts	Oregon
Delaware	Minnesota	Pennsylvania
District of Columbia	Mississippi	Rhode Island
Florida	Missouri	South Carolina
Georgia	Nebraska	South Dakota
Illinois	New Hampshire	Tennessee
Indiana	New Jersey	Vermont
Iowa	New York	Virginia
Kansas	North Carolina	West Virginia
Kentucky		Wisconsin

The most severe infections have been reported in Kentucky, Tennessee, Missouri, Illinois, Virginia and West Virginia. Heald (1933, p.797) states: "The unusual development of the disease in such states as Iowa and Nebraska seems to be due to two factors: first, the fairly common practice of planting the cedar tree as a windbreak around orchards and as ornamental trees for the home grounds; second, to the frequent use of a very susceptible variety, the Wealthy. In Virginia and West Virginia, the common cedar is very much at home, as its name indicates, <u>Juniperus virginiana</u>, and is

frequent along the roadsides even in the commercial apple districts. This natural distribution of the cedar and its ready reproduction, coupled with the extensive plantings of another very susceptible variety of apple, the York Imperial, gives ideal conditions and cedar rust thrives and waxes fat and multiplies." (Fromme, 1918, p.2)

H. Economic Importance

East of the Rocky Mountains, the widespread incidence of rust so seriously threatens the productiveness of apple orchards that it is of almost equal concern to commercial growers as fire blight or apple scab. Individual researchers differ as to the precise importance of rust in destructiveness. Pammel (1905, p.36) calls cedar apple fungus "very destructive". Hamilton (p.3) emphasizes that it causes "heavy annual losses and rapid degeneration of blocks of infested trees"; Weimer (1917, p.510) speaks of its localization stating that the southern states "where cedars grow in close proximity to the orchards, the disease causes an annual loss of several hundreds of thousands of dollars and there is considerable evidence that it is becoming more destructive each year"; Emerson (1905) speaking of Nebraska, G. E. Stone (1911) of Massachusetts, and Giddings and Neal (1913) of West Virginia all underline its annual increase in seriousness; Stewart (1910) records a few outbreaks in New York but says "the disease is

rarely of much economic importance"; on the contrary, R.E. Stone (1908) in Alabama and Reed and Crabill (1915) in Virginia list this as the most serious disease of apples in their respective states.

The disease has become severe enough to necessitate preventive measures only comparatively recently. In fact, the responsible organism was first described by Schweinitz in 1822. Pammel had never observed rust on cultivated trees in Iowa before 1905. Orchards in Virginia, West Virginia, Iowa and Nebraska have been particularly infected. Fromme (1918) writing of conditions in Virginia, says: "The attack of cedar rust on the Imperial York variety is chiefly on the foliage which falls early, leaving half-nourished under-sized apples. When the infection is heavy, the loss is almost complete. Promising number ones are reduced to culls. The tree itself suffers severely. Growth is arrested, few fruit buds are formed and the next year's crop is sure to be a light one. A heavy cedar rust infection thus means a loss of a large part of two years' crops."

In 1912, Virginia and West Virginia experienced an unprecedented infection of cedar rust causing tremendous damage to the apple crop. Various writers estimated the financial loss to growers in individual counties from $75,000 upward. This emphasizes the importance of rust as a factor in commercial orchard districts. However, this does not include the potential damage done to the trees. Not only the current crop must be accounted a loss, but also the sapping of the trees'

vitality must surely lessen each succeeding crop. Too, this devitalization leaves the tree more susceptible to other disease caused by insects or fungi. In the case of the York variety cited above, the trees were so weakened by successive infections that a majority of young specimens died before reaching bearing age. This led to the belief that that variety was running out. However, it was shown that such trees, if protected from the disease, could resume their normal growth and could produce representative crops of apples.

A curious situation was uncovered in an experiment carried on by Weimer in central New York State. Historically, in this locality the disease is rampant on wild species of apples but is rarely found on cultivated varieties. Weimer observed two orchards during the 1914 and 1915 seasons. One of these had cedar trees heavily infected with G. Juniperus-virginianae, G. globusum and G. clavipes growing among the apple trees and the other had a grove of similarly heavily infected cedar trees a half-mile distant. The only damage to the orchards to be discerned was two affected apples and a few affected leaves. Weimer ascribed this to the fact that factors other than close proximity of the two hosts were responsible in the spread and intensity of infection.

Although cedar trees are materially injured by apple rust, the greatest economic loss occurs in the apple trees. Not only the loss of the current crop is serious, but perhaps even more important is the gradually reduced efficiency of the trees through premature defoliation and impaired vigor leading to

their probable premature death.

According to the United States Dispensatory (18th Edition, p. 1699) cedar galls are popularly used as anthelmintic in doses of 0.65 to 1.3 grams three times per day. The treatment is not official and is not given in the United States Pharmacopoeia.

I. Legislation

After the severe epidemics of cedar apple rust had ravaged the commercial apple orchards of Virginia in 1910 and 1912, there was proposed a measure to list the red cedar as a pest and to seek legislation empowering its destruction where it was a menace. Reed, Cooley and Crabill (1914, p.26) stated; "Some such measure would undoubtedly be desirable in cases where apple growers suffer from infection coming from neighboring farms, especially from farms on which apples are not grown commercially. Many instances are known in which the owner of cedars has refused to cut or even to sell the privilege of cutting cedar trees which are of no commercial value whatever. Often the cedars are mere bushes growing in fence corners or on barren hillsides where they would never grow large enough to be used as timber or posts; however, these same bushes may produce enough infective material to spread disease to many acres of orchards and destroy thousands of dollars worth of apples. This is undoubtedly an unjust state of affairs."

As a result, a special Cedar Rust Law was enacted and became effective in late 1914. By this law, a district enjoys "cedar local option". In areas where cedar eradication was employed, beneficial results were observed. However, there were many protests against the law by powerful land-owners and the complete success of the eradication program became jeopardized. Workers were often unable to make complete surveys of existing cedar trees because irate landownere would not allow access to their property. The next countermove toward success in the program was an urgent request for legislation empowering the Crop Pest Commission to enter private property and destroy red cedars wherever they were a menace to the apple growing industry in order to control the situation in certain localities.

W. E. Rumsey, in the First Biennial Report of the State Crop Pest Commission covering the period from March 1, 1913 to June 30, 1914 (p.38), announced; "On account of the opposition encountered in cutting cedar trees to prevent damage to apple crops, the Commission adopted the following policy; In sections where the apple industry has developed sufficiently to warrant the condemning of cedar trees as a nuisance,on account of such harboring one stage of a disease seriously injurious to apple crops, such cedars must be destroyed or the balls (galls) removed thereon. Where there is but an isolated apple orchard here and there in a section where cedars are exceedingly abundant, then no action is to be taken toward destroying the cedar trees."

Fromme (1918, p. 7) called "cedar eradication the cheapest form of orchard insurance you can buy."

Brook (1930, p.327) stated; "Most excellent results have been obtained by the destruction of cedar trees although many protests have been made by owners of cedars."

Heald (1933, p.810) termed the eradication of the cedar "the most effective and most economical method of cedar-rust prevention. The cutting out of cedars in Virginia and West Virginia has been practiced in many sections with excellent results and at an average cost of less than fifty cents per acre.

II. The Causal Organism

A. Taxonomy

Gymnosporangium juniperi-virginianae is a fungus belonging to the rust group or _Uredinales_. This order shows certain affinities to the true basidium fungi and as a consequence has sometimes been known as _Protobasidiomycetes_. The general characteristics of the _Uredinales_ according to Heald (1933, p. 762) are "(1) an intercellular, branched septate mycelium (more rarely intracellular) containing yellowish or orange-red oil drops; (2) polymorphism of spores, typical rusts producing a succession of five different forms in the course of the life cycle; (3) the germination of the teliospore to form a _promycelium_, or a sporulating stage independent of the host rather than the direct production of an infection hypha; and (4) the development in certain species of heteroecism or the separation of the spore forms on two separate and unrelated hosts."

The genus _Gymnosporangium_ belongs to Family _Pucciniaceae_. Heald (1933, p.770) summarizes the chief characteristics of the family as follows: "Telia erumpent or covered, teliospores one to several-celled, borne singly on a pedicel or in groups, free or imbedded in a gelatinous matrix and dark colored or nearly colorless. Germination by the formation of typical promycelia. Urediniospores always solitary. Aecia with or without peridium. The family shows all degrees of polymorphism, various degrees of heteroecism and the most complete

physiological specialization or differentiation of biological species that is known among fungi."

The genus Gymnosporangium has teliospores two or more celled by transverse partitions. The teliospores are embedded in a gelatinous matrix.

Arthur in the North American Flora recognizes Aecidiaceae as synonymous with the Pucciniaceae. (1934)

The species under discussion has teliospores two-celled in a gelatinous matrix. The telia are golden yellow, cylindrical, acuminate and vary in length from less than one-half inch to more than one inch. The teliospores are oval to acuminate, frequently constricted at the cross septum and 15 to 20μ by 46 to 60μ. The promycelium is usually four septate leaving a sterile stalk cell and four fertile or basidial cells, each of which produces a secondary spore or sporidium borne on a short lateral projection called a sterigma. A teliospore thus produces eight sporidia.

B. Morphology

1. Cedar

The normal cedar leaf is for the greater part of its length tightly attached to the twig. Only the apical portion is free.

Mohr (1901, p.18) states that, "the epidermis consists of a layer of flattened elongated cells with rather thick

walls, communication by simple pits, and on the inner side of the free part of the leaves, the epidermis is covered by numerous stomata. On the dorsal side of the leaf, the epidermis is underlaid by a simple layer of strengthening sclerenchymatous cells, which are doubled in the corners and also on both sides of the glands, over which the hypodermal layer does not extend. On each side of the fibrovascular bundle is placed a group of tracheid-like elongated cells with lignified walls and bordered pits as is also seen on each side above and below the vascular bundle of the common leaf axis. These tracheid-like cells show more or less peculiarly curved projections from their walls, a feature characteristic of the dorso-ventral leaved section of Juniperus. The fibrovascular bundle passes along the ventral side of the gland and contains, on the border, scalariform cells. The parenchymatous tissue is loose, composed of large cells, the palisades, normal to the surface."

An examination of Diagram 2 (Appendix) will readily show that the ventral surface of the epidermis of the cedar needle will prevent infection. In this region, the hard unbroken protecting sclerenchymatous layer underlies the epidermis and the smooth surface of the epidermis is devoid of stomata. On the other hand, the mesial surface of the cedar needle is very well adapted to multiply the possibilities of infection. The axil of the needles forms a natural pocket to collect and hold spores and water to aid in germination of the spores when temperature conditions become favorable. The spore tubes have only a thin epidermal layer with numerous stomata to penetrate.

The infection of the inner side of the needle by the aeciospores results in the production of a cedar apple. The cedar apple is merely an hypertrophy of a cedar leaf infected by the fungus G. juniperi-virginianae. Structurally, their tissues are quite similar to those of the cedar apple, which is a distorted modification of the normal leaf tissues.

Heald first showed that "cedar apples" appear on the cedar trees before the aeciospores of that season have been dispersed. This, of course, can only mean that the galls had resulted from the previous year's infection of aeciospores. Whether the aeciospores infect the cedars as soon as they are dispersed in the fall or whether they overwinter and infect the tree in the spring has not been conclusively determined. "Even if the aeciospores should lie dormant in the leaf axils during the winter period, it means that the pathogene requires approximately 23 months from the time of aeciospore dissemination to complete its life cycle." (Heald, p.807)

When the inner surface of the cedar needle is infected by the aeciospores, the parenchyma of the leaf is stimulated to excessive growth. The fibrovascular bundles become greatly contorted and radiate in an irregular manner throughout the developing gall. An examination of the tissues of a "cedar apple" will reveal four primary tissues; (1) the hypertrophied parenchyma, (2) the contorted fibrovascular tissue, (3) a layer of heavy thick tissue called the cortex or rind, (4) the fungus.

Sanford (1888, p.263) gives the best description of the

tissues of the cedar apple. "The parenchyma, which is a modification of the cedar leaf parenchyma, makes up the greater portion of the cedar apple. It consists of a mass of cells which are continuous with and similar to the normal parenchyma of the cedar leaf, except that, as a result of the stimulation of the fungus, they have attained a relatively enormous size. They measure up to 90 x 150μ, while the normal parenchyma cells of the cedar leaf measure on a maximum about 30 x 80μ. They are thin-walled and are for the most part oblong-oval in shape and lie with their long axes coincident with the radii of the cedar apple. They are as closely packed as their oval shape allows, but owing to their large size, the intercellular spaces are also large. The nuclei of these cells measure about 10 x 20μ and contain either one or two nucleoli. In some sections, the nuclei of the cells are binucleate. This doubling of the nucleoli is not explained except, perhaps, as an indication of vigorous growth."

The parenchyma cells are all packed with starch grains up to the time that teliospore production begins. At this time, the starch begins to disappear from the cells immediately beneath the teliospores. This dissolution of the starch progresses gradually until at the end of the spore-producing period, no starch remains in the parenchymatous tissue. Since the dissolution of the starch and the formation of the telio-spores begin together, it seems logical to assume that the fungus is drawing on this store of starch for the formation of spores. Probably an amylase is produced at this time which

converts the starch into sugars available for the fungus.

The walls of the parenchyma cells are composed entirely of cellulose, at least until late spring, as shown by their positive reaction to iodine and sulphuric acid and negative reaction to phloroglucin.

The fibro-vascular system is a modified continuation of the fibro-vascular system of the cedar leaf. From or near the base of the "cedar apple" where the vascular elements are much contorted, arise many branches which extend radially almost to the cortex. The simplest fibro-vascular bundle is composed of a bundle of spiral tracheids, a bundle of the bordered pitted vessels characteristic of conifers, and a sheath of much elongated parenchyma cells. The more complex vascular bundles may contain several bundles of tracheids and bordered pitted vessels bound together and surrounded by elongated parenchyma cells.

The cortex is a layer 4 to 6 cells thick which covers the "cedar apple". Prior to the rupture of the teliosori, the cortex is thickest over the fruiting bodies. The cortical cells are empty, irregularly compressed and exhibit all the characteristics of dead cells.

The fungus mycelium is found occupying a portion of the intercellular spaces between the parenchyma cells. The mycelial threads ramify throughout the "cedar apple" and grow, for the most part, appressed to the walls of the host cells. The branching of this mycelium is peculiar, the tendency of the strands is to grow in straight lines and there is some

indication of anastomosing. The cells of this mycelium are of binucleate nature. The septa between cells are very thin and hard.

The mycelium is most abundant just inside the cortex of the "cedar apple". At the base of the teliosorus, it forms a compact mass crowding the host cells almost out of existence. At the base of the "cedar apple", the mycelium is much contorted, quite large in diameter, occupying all the space between the host cells.

It seems to be usual to find the entire leaf from which the gall originates to be permeated with mycelium even before much hypertrophy or other change becomes evident.

Weimer incorrectly cites Sanford as thinking that no cross walls are found in the hyphae. (1917, p.518) A study of the literature reveals that Sanford (1888, p.263) was aware that "thin, very hard" septa exist. Weimer says, "The septa are often difficult to locate." In general, the hyphae average in width about 2.5μ.

Haustoria are present but not abundantly in the young galls. Reed and Crabill (1915, p.27) give a detailed account of the formation of haustoria. They were able to find only the very early stages in the autumn and believe that mature haustoria are not developed until just preceding teliospore formation in the spring.

The mature gall has a corky appearance on the exterior with a number of circular depressions. In the spring, depending on the latitude and weather conditions, the cortex

ruptures at the depressions noted and tentacles or telia emerge. When completely expanded, the telia are orange colored gelatinous masses which may be more than one inch in length. The telia have teliospores embedded in them which germinate during warm spring rains. The teliospores are two-celled, ovate to acuminate, and slightly constricted in the middle; the apex is somewhat papillate. Each cell of a teliospore develops a hypha-like structure called a promycelium which typically has four fertile basidial cells and a short projection called a sterigma holds a single secondary spore or sporidium. In the period following a rainy period, the sporidia part from their sterigma and are carried by the air away from the cedar.

C. Germination of Spores (Teliospores)

Coons (1912, p.217) conducted some detailed studies on the development and discharge of sporidia and was the first to call attention to their forcible discharge. He said, "The process of putting out germ tubes requires from six to fifteen hours." Fulton (1913, p.62) reported some investigations as to the factors which influence sporidia production and stated that, "From the first swelling of the gelatinous horns to the formation of infection spores, about twenty-four hours of moisture are required." Reed and Crabill (1915, p.28) found that, "A teliospore must be covered with a good film of water or suspended in water at optimum temperatures" in order to

secure germination. Giddings and Berg (1916) studied the factors inducing sporidia discharge, noted the forcible ejection of sporidia and secured abundant sporidia discharge in less than three hours after first moistening galls. Weimer (1917) studied sporidia development and discharge and observed that the telial horns must be kept moist from four to five hours.

Hamilton (1937, p.8) states, "Generally the galls of the apple rust fungus on the cedar begin the production of the teliospore-bearing horns by early May (New York). The teliospores, with wetting, germinate immediately or shortly after their appearance, producing basidiospores. The minimum temperature for teliospore germination has been reported variously at 40 to 53°F, with an optimum range at 60 to 73°F. The basidiospores are discharged from the surface of the gelatinous masses with warm rains. Basidiospore discharges take place at an apparent minimum temperature of about 50°F, although 30°F has been reported."

Hamilton found that galls may liberate basidiospores when soaked with rain for thirty minutes or less although admitting heavier discharges result from rains of two or three hours duration. This observation greatly reduces the time given by such men as Fulton, Weimer, Giddings and Berg.

Unless the rain is protracted, the spores are not liberated without lowered humidity.

D. Inoculation

The Rikers (1936, p.52) state in general; "The natural modes of entrance of disease producing microorganisms or pathogenes into their host plants or suscepts deserve attention before inoculation methods are considered. Among these natural modes are the following:

(1) wounds, including those caused by

(a) insects, animals, and cultivation

(b) agricultural procedures, e.g. grafting and pruning

(c) weather

(2) natural openings or relatively unprotected parts including root hairs, growing tips of roots, lenticels, stomata, hydathodes, growing tips of shoots and flowers

(3) direct penetration, including mechanical, chemical and perhaps mass action."

The susceptibility of the host plant may be influenced by a variety of factors including:

(1) plant factors

(2) parasitic factors

(3) environmental factors

Among the plant factors are age, vigor, previous treatment, e.g. vernalization, previous inoculation, radiation and moisture; subsequent treatment, e.g. environment during incubation; morphological condition, e.g. stomatal openings and protective tissues; physiological conditions; e.g.

carbohydrate-nitrogen ratio, osmotic pressure, and pH; and strain variations. In trials to compare the susceptibility of different varieties, it is often necessary to make preliminary tests to determine the suitable time for inoculations. Because the varieties may have different rates of growth, two or more successive inoculations may be needed to reach all the varieties at a susceptible stage.

Many of the items listed above under plant factors apply similarly to the pathogenic organism. Susceptibility and pathogenicity are mutually interdependent.

Environmental factors such as temperature, moisture, light and soil nutrients must be considered.

Plants for inoculation studies are commonly grown in the field where there is little control over conditions or in the greenhouse where many environmental factors may be rigidly controlled. Two other factors that frequently cause trouble in the greenhouse deserve mention.

(1) Extremely small amounts of illuminating gas prevent normal growth of many plants.

(2) Fertile soil which has been stored over winter in the greenhouse in a moist and warm condition may be acted upon by nitrifying bacteria so that it becomes toxic to a large number of plants. Sometimes it is desirable to grow plants for inoculative studies so that all undesired microorganisms are excluded.

Detached leaves have been used most commonly for inoculation studies of this fungus. They can frequently be

kept alive on sugar solution for some time in relatively good condition.

Greenhouse studies of various plants are limited in season by the rest period or dormancy of the plant.

Artificial inoculations can be made in a variety of ways which more or less simulate natural inoculations or which may sometimes be considerably more drastic. The two most common methods used in connection with the cedar rust fungus are dusting and spraying. In dusting, the fungus spores are applied on the leaves of susceptible host plants. Since adequate moisture is desirable for leaf infection, spraying is more common.

Suspensions of fungus spores are sprayed on the surfaces of susceptible leaves and stems. Several devices aid in securing better infection. The relative humidity of the air surrounding the host plant is controlled both before and after inoculation. The time depends upon the host plant and parasite.

Prince and Steinmetz (1940, p.2) in studying the host relationships of Gymnosporangium rusts in Maine used the following technique which was a modification of the method used by Hubert in 1916.

"The telial material was collected and placed in a refrigerator in which the temperature was maintained at approximately five degrees centigrade. Heavily infected parts of the host were prepared for the inoculum by placing portions of the twigs in jars partly filled with distilled water. The telia were kept in the jars until an abundance of the basidiospores

were observed in freshly prepared spore suspensions. The twigs of the branch of the test plants, which were usually selected beforehand, were loosely tied in order to provide a more compact mass of leaves. Absorbent cotton was then wrapped around the branch where an improvised cellophane cylinder was to be fastened. The lower end of the cellophane sheet was wrapped around the cotton and tied so that a trough could be shaped under the plant parts. After these parts were moistened with distilled water, the inoculum was applied directly with a clean piece of wet cotton or with a portion of telial host. Additional wet cotton and water was placed in the improvised trough. The cellophane cylinder was secured by folds and fastened with twine in order to maintain as near as possible a saturated atmosphere about the inoculated leaves. The inoculated chambers were shaded by means of paper bags. These chambers were removed at the end of 36 to 72 hours."

Farlow (1885, p.311) working with live species of Gymnosporangium, produced pycnia on detached leaves of Crataegus and Amelanchier with three of the species under the conditions quoted as follows: "The leaves (Pomaceae) were placed on moistened glass slides and arranged on zinc stands under bell-glasses. The sporidia were then carefully dropped upon the leaves which were immediately covered by a bell-glass. The leaves under each glass were sown by the sporidia of but one species, the bell-glasses were removed for only a moment and at no time were the leaves under more than one bell-glass exposed."

Coons (1912, p.222) in 1912 made inoculations in Petri dishes with <u>Gymnosporangium juniperi-virginianae</u> on apple leaves to determine the method of entrance of the germ tube.

Reed and Crabill (1915, p.43) conducted five series of inoculations of apple leaves and found that only young leaves are susceptible and that infection takes place only in the presence of abundant moisture.

Weimer (1917, p.516) records: "On July 30, 1915, a small cedar apple was found on a cedar tree that had been inoculated on July 25, 1914 by suspending over the tree the fruit of an apple infected with <u>Gymnosporangium juniperi-virginianae</u>. When first observed, this gall was one millimeter in diameter, globose, and green in color. It appeared to be developing from the upper or inner side of a small scale leaf. This small tree was brought into the greenhouse in the early spring of 1914 and all cedar apples were removed. It was carefully examined on April 10,1915 for any signs of cedar apples and none were observed. That this gall could have been the result of natural infection before the tree was removed to the greenhouse seems impossible, since in that case it would have developed in the previous year. By October 1, the gall had doubled in size and spores were produced in February of 1916. Apparently the gall resulted from the inoculation. It is, however, impossible to determine this point absolutely.

Clinton and McCormick (1924, p.491) have done much work on this question. The following spore fruits are produced in succession by a typical rust and each stage may be

indicated by a symbol.

Symbol	Spore Fruits	Spores	Stage
O	Pycnia	Pycniospores	Cluster cup
I	Aecia	Aeciospores	Cluster cup
II	Uredinia	Urediospores	Red rust
III	Telia	Teliospores	Black rust
IV	Basidia	Basidiospores	

A rust may develop all types of spores (O, I, II, III and IV sporidia) in the course of its life cycle, or some species may omit one or more forms.

In the apple rust, the spore stages are not autoecious but have become separated on two distinct hosts. This condition is known as heteroecism. The O and I stages in apple rust are found on the wild crabs and the cultivated varieties of apples. The III stage is found only on the *Juniperus virginiana*, *Juniperus barbadensis*, etc.

In Clinton and McCormick's work, inoculations with the O stage were made on a host known to be very susceptible. There were no results, which seemed to indicate that the O stage is not a means of spreading the rust. Inoculations with the III stage were successful on *Pyrus ioensis* and *Pyrus malus* only. All three inoculations took on the Bechtel's Flowering Crab which is a very susceptible species. On *Pyrus malus*, however, the results varied with the different species used, failing on Baldwin, Gravenstein, McIntosh and Northern Spy;

taking poorly on Fall Pippin, Greening King, and Sutton's Beauty; taking well on Duchess, Oldenburg, Hurlburt, Russet, and Wealthy. These results agree well with the observations of workers on field trees. The method used by Clinton and McCormick was a modification of the Petri dish method. It seemed effective and at the same time simple. They filed four opposite or equally distant notches about a quarter of an inch deep in the edge of the bottom dish and stretched rubber bands across and diagonally through these to hold the leaves out of the water placed below but free from pressure above. A small amount of water was poured in the bottom of the dish. The spores were dusted or brushed off the inoculating material over the exposed surfaces of the leaf. The Petri dishes were placed where they received favorable light for plant growth. Fifty-two percent of the inoculation of _Pyrus malus_ were successful with the III stage.

A good deal of work has been done by Crowell (1934) on this subject in the Arnold Arboretum, Massachusetts. Inoculations were made on 108 species of eleven genera of plants and the results tabulated. The genera were _Amelanchier_, _Comptonia_, _Crataegomespilus_, _Cydonia_, _Malus_, _Myrica_, _Photinia_, _Pyrus_, _Sorbaronia_, _Sorbopyrus_, and _Sorbus_. In the field, Crowell made observations on 942 species of _Crataegus_. His results were as follows:

(1) "All the species and varieties of the section _Chloromeles_ of the genus _Malus_ and two others, namely _M. fusca_ and _M. sylvestris_, produced aecia. The hosts showed

differences in their degree of susceptibility to the fungus.

(2) "Twelve species and varieties found in other sections of genus Malus produced spermogonia only. The infection spots were always few and the spermogonia were very irregular both in their time and in their manner of development.

(3) "Other species and varieties of Malus (47 in number) and all other species tested or observed were found to be immune.

(4) "The hosts on which aecia were produced were found to be susceptible for various periods of time. The most susceptible species could be infected throughout the greater part of the growing season. The less susceptible ones could be infected for progressively shorter periods down to about two weeks."

III. Epidemiology

A. Dissemination of Sporidia to Pomaceous Host

The study of the dissemination of spores is important in epidemics caused by fungi. Moisture is the most important single factor for spore discharge, but other factors including temperature may influence dispersal. The main agent in the dispersal of sporidia to its pomaceous host is the wind. It is important, therefore, to determine the frequency of spores in the air.

An attempt was made by Reed and Crabill (1915, p.12) to make some records of the number of sporidia dispersed by the cedar galls and to determine what distances the spores are carried in the wind. While the results that were obtained by these workers were only roughly quantitative, certain facts were apparent.

(1) The number of sporidia dispersed tended to become successively smaller on fair days following rain.

(2) The sporidia seem to be present at all times in the air in small numbers.

(3) The number of sporidia found in the air decreases gradually for a distance of about 800 meters (approximately half a mile) from the source of the infection. Chance of infection beyond this point would be slight.

The method used most successfully by Reed and Crabill to "trap" the sporidia was as follows: "Large dinner plates filled with distilled water were set on six foot poles to

approximate the conditions of leaves on the lower branches of apple trees. The sporidia were obtained by centrifuging."

Glass slides, covered with adhesive material such as vaseline or glycerin, were tried but found unsatisfactory.

Information regarding dissemination of spores is most important. In states which have laws which permit the destruction of the cedars within certain distances of commercial orchards, this information would have special significance.

Reed and Crabill (1915, p.14) counted the number of infections per twig at varying distances from the cedar and found, as would be natural, that rust infection decreased rapidly as the distance from the cedars increased. The number of infections per twig at 50 meters were 38.8. This figure was too low as many of the worst infected leaves had already fallen from the trees. At 100 meters, the number of infections had dropped to 34.7; at 200 meters to 7.9; at 300 meters to 4.2. The young leaves were most infected.

McLachlan (1935, p.61) made an attempt to determine at what levels spores may be found. His collection trip by airplane between Waltham and Cochituate, Massachusetts revealed spores are present in early May up to altitudes of at least 2000 feet during rainy periods. During such normal dispersal periods, the spores were found to be viable for many days.

McLachlan carried on his work to determine the percentage of spore germination at different temperatures and humidity conditions for varying lengths of time with the following results:

(1) Spores at all temperatures at 0% humidity were killed within 22 hours.

(2) Spores above a temperature of 30°C died in 22 hours under all humidity conditions.

(3) Spores below a temperature of 25°C and above a humidity of 25% could live a sufficient length of time to be dispersed for many miles in a viable condition.

(4) Spores below a temperature of 10°C could remain viable more than seven days.

(5) Spores at 5°C and high humidities could live more than twenty-five days.

1. Influence of Environment on Infection

To a large extent, weather conditions govern the amount of rust in any specific season. The germination of teliospores and the infection of the aecial host require moisture and therefore the number of rain periods governs the number of infection periods.

Weimer experimented on this phase of the problem, attempting to determine the approximate amount of moisture necessary for infection of the aecial host. He found that only a little moisture sufficed. There must be sufficient moisture to cause the telial horns to gelatinize and to keep them in that state from four to five hours. This period should be followed by one of high humidity in order to furnish the necessary moisture

for infection.

This is contrary to the opinion of Reed and Crabill (1915) who state that infection takes place only in the presence of abundant moisture. It is not clear whether their intention is to include the whole process of basidiospore formation and infection or only the latter, since they also make the statement that infections followed short periods of rainfall.

In 1911, it was remarked that trees that had suffered injury to their roots by wooly aphis (Schizoneura) and therefore were in a generally weakened condition showed noticeably more rust infection than other trees of the same variety in the same orchard.

2. Relations of Susceptibility to Infection

Observations have been made in the different states on the comparative varieties of apples. Giddings and Berg (1915) recognize these classifications:

"1. susceptible

2. moderately susceptible

3. resistant

4. immune"

Some varieties fall in different classes in different states; for example, the Ben Davis was found susceptible in Virginia and Iowa; fairly susceptible in West Virginia; and resistant in Massachusetts, Rhode Island, Delaware and

Nebraska. Manifestly, resistance may be seeming rather than real since some varieties may avoid infection simply through the chance development of their foliage at inopportune times. It seems questionable that any varieties are truly immune.

There does, however, seem to be general agreement that certain apples are very susceptible or very resistant if not, indeed, immune. Between the two extremes,one finds disagreement between workers. There seems to be no question that commercially valuable apples such as the Wealthy, York Imperial and Jonathan are very susceptible. Varieties at the other extreme such as the Baldwin, Stayman, Winesap, Arkansas Black and Yellow Transparent are reported as resistant in most localities and immune in West Virginia.

Halsted, in 1889, considered the possibility of some varieties of cultivated apples being more susceptible than others. He said (p.380) "very likely some varieties of cultivated apples are more susceptible to rust than others, but as the observations upon this point are very meagre and fragmentary, it is not safe to draw general conclusions from them."

Shortly after this, Stewart and Carver (1896, p.538) set out to determine why the cultivated crab in central Iowa should be free from Roestelia. They made inoculations upon the wild crab, Pyrus coronaria and upon cultivated varieties at Ames. The experiment at Long Island gave evidence that some varieties were wholly exempt from Roestelia, which indicated that its

absence on cultivated apples in Iowa might not be entirely due to unfavorable weather conditions, but chiefly to the fact that the varieties grown in Iowa were not susceptible.

Fulton (1913, p.62) published the results of some inoculation experiments which showed the development of immunity in apple leaves of susceptible varieties and the same fact is mentioned by Reed, Cooley and Crabill in 1914.

Smith's Cider is reported by Reed and Crabill (1915, p.40) as being affected by the rust not only in the leaves, but also in the younger twigs. They noted the varietal susceptibility of various apples at this time. The York Imperial, Northern Spy, Jonathan, Bonum, Rome and Ben Davis were listed as very susceptible. Winesap, Stayman, Arkansas, Yellow Newtown, Northweston Greening and Grimes were practically immune. Nearly all the common early summer apples showed a high degree of resistance. A comparative study of the foliage of susceptible and resistant varieties was made by Reed and Crabill to see if any morphological differences could be detected. Microtome sections of leaves of the same age showed no distinguishable differences in thickness of epidermis, character of stomata or any other property which was more constant for any one variety than any other.

Hairiness of leaves was next considered. Hairs, they reasoned, might perhaps give lodgement for sporidia. It was therefore thought possible that the abundance of hairs might influence the number of infections. Four of the most susceptible

varieties were compared with three of the most resistant. Leaves of the same age and positions of the twigs were examined. Both upper and lower surfaces were examined. Some of the most resistant ones were as hairy as the most susceptible and vice-versa. No correlation could be discerned between susceptibility and hairiness of leaves.

Hopkins, in 1922, recorded a case of heavy twig infection on the Yellow Bellflower.

Young, in 1927, reported severe injury to young Ada Red trees in Arkansas with the resultant death of the twig tips. Older trees of this species sometimes were affected.

Inoculation experiments conducted by Thomas and Mills (1929, p.20) on the susceptibility of McIntosh and Wealthy leaves show that the fungus made its way with equal ease into both types of leaves but that the development ceased in the McIntosh before pycnia were formed.

Bliss (1933) reported that the following apples were subject to twig attacks but produced only spermogonia: Arkansas, Benoni, Jonathan, Malinda, Okabena, Peerless, Red Astrachan, Stayman, Twenty Ounce, Wagener, Whitney and Winter Banana.

Crowell (1934, p.181) found the following orchard varieties of apples to be susceptible to fruit attack by Gymnosporangium juniperi-virginianae, Schw.: Ben Davis, Delicious, Early Harvest Esopus, Gideon, Grimes, Jonathan, Oldenburg, Red Delicious, Red June, Rome, Sutton, Twenty Ounce, Wealthy, Winesap, Winter Banana, Yellow Bellflower, Yellow Transparent

and York. The following are listed by the writer as subject to twig attack: Ada Red, Duchess, Golden Delicious, Missouri Pippen, Red June, Rome, Salome, Smith Cider, Wealthy, Yellow Bellflower and all varieties listed above by Bliss.

It is believed that the apparent contradictions among workers are due to one or several of the following sources of error:

(1) The relative abundance of the fungi in the years that the data was collected.

(2) The distance of apple trees from cedar trees.

(3) Strains of cedar apple rust fungi.

(4) Variation in the susceptibility with varieties of apples.

(5) Improper identification of the variety of apple.

(6) The personal element in evaluating relative susceptibility.

3. Factors Opposing Entrance

Very little literature is available which discusses the factors opposing the entrance of the parasite into the host. In general, however, certain suggested reasons for disease resistance are noted for all plant diseases of this type with more experimentation needed to determine if they apply to this particular case. The resistance of the plant to the parasite is thought to be either a mechanical or a physiological resistance. Certain external and mechanical characters such

as hairiness have been investigated by Reed and Crabill. No evidence was found to indicate that the hairs served as either a barrier or help to infection. Other points needing further study include: amount of waxy layer, thickness of bark layers, internal characters such as thickening of the cell walls, composition of the middle lamella, and formation of wound materials.

Physiological resistance has been reported associated with factors like osmotic pressure, cell-sap acidity, tannin, lack of proper nutrients, substances toxic to the parasite, and substances neutralizing parasitic action.

Probably, various combinations of factors enter into a given case as the concepts of resistance and of parasitism complement one another.

In 1915, Reed and Crabill showed that only young apple leaves were capable of infection. This they attributed to the lack of development of the cuticle of the leaf.

B. Location of Parasite in Apple

1. Intimate Relations of Apple and Parasite.

a. Morphology

Coons (1912, p.215) determined that the sporidia germ tubes pass through the cuticle of the upper surface of the leaf. This view, which contradicted the published work of Heald (1909), placed a greater emphasis upon the study of the normal and diseased apple leaf. It is now well established

that stomatal infection is not true here. Only the germ tubes from uredospores and aeciospores seem to pass through the stomates.

(1) The mycelium

The mycelium of the parasite in the pomaceous host is very similar to that found in the hypertrophied gall on the cedar tree. The chief difference found is that the mycelium of the apple leaf is gametophytic instead of sporophytic, i.e. uninucleate rather than binucleate. The diameter of the two forms is about the same.

After infection takes place, the mycelium moves from the point of entry into the intercellular spaces through many ramifications. Haustoria are sent into the palisade and spongy tissue cells of the host. The stimulation of the filamentous haustoria on these two types of cells brings about great changes within the leaf structure particularly within the spongy parenchyma layer. The palisade cells enlarge slightly and appear little altered otherwise. The spongy cells, however, change their shape, position, and multiply rapidly. Their appearance becomes quite similar to the palisade cells as they elongate and arrange themselves perpendicularly to the upper epidermis. At first glance they appear much like a continuation of the palisade layer.

The intercellular spaces in the spongy parenchyma layer entirely disappear. While there is no injury to the epidermal

layer as a whole, the areas around the spermogonia on the dorsal aspect and the aecia on the ventral aspect are greatly affected and modified. These affected epidermal cells collapse with a possible resultant drop in transpiration. This point was the subject of much discussion by Reed and Crabill. They felt while the stomata on the lower epidermis were not directly affected by the haustoria, that the obliteration of the intercellular and substomal spaces could largely account for the lowered ability of the leaf to transpire.

(2) The spermogonia

About a month after the sporidia germ tubes have punctured the dorsal cuticle, the apple leaf shows small spots, usually orange-yellow in color. Spermogonia appear on these spots and exude a sweet sticky liquid. The writer has often seen ants feeding upon this material. It seems to have a rather stimulating effect upon them. In 1887, Thaxter (p.259) recorded that flies were observed feeding upon the exudate. Reed and Crabill (1915, p.63) stated: "The spermogonia are formed immediately under the upper epidermis of the apple leaf. A dense mass of short-celled mycelium collects at this point and grows until a size of about 130 x 120μ is attained. As development goes on, the mycelium is seen to arrange itself into strands approaching a point at the apex which is to be later the ostiole. No distinct wall is present in the spermagonia, the strands which give rise to the spermatia being

continuous with the cells which ramify between the host cells. At maturity, the spermogonium ruptures the overlying epidermis, the fungus strands are somewhat protruded and by obstriction, the spermatia are cut off from these strands. The spermatia are thus continuously produced until all the mycelium of the spermogonium is used up and only a hollow space remains under the epidermis. The spermatia are ovate to club-shaped and measure 2 x 6μ. Repeated attempts to germinate these spores have failed."

(3) The aecium

A rounded clump of mycelium in the area immediately beneath the palisade layer begins to swell and elongate toward the lower epidermis. When the lower epidermis is reached, the epidermis ruptures and a small brown papilla protrudes which grows until it becomes about half a millimeter in length. The outermost aeciospores have become modified into peridial cells. The splitting of the peridial cells to set free the aeciospores has been described by Kern (1910, p.445). He describes the peridium as a single layer of cells which forms a covering for the aeciospores within. The peridial cells are virtually modified aeciospores and are produced by a differentiation of the apical aeciospores at the top of the aecidium and of whole chains of aeciospores on the sides of the aecium.

The peridial cells are diamond shaped when seen from below. They are oblong when viewed from the side. The cells

are firmly joined together with the basal end of each cell overlapping the upper end of the cell about it. The separate cells form strips which are rather loosely bound one to another. When the peridium ruptures, the split always occurs between the strips of cells. The peridial cells forming the peridial strands have been estimated by Pammel (1905, p.18) to be 90 to 110μ long with transverse striae.

Moisture greatly affects the peridial strand. When it is dry, the peridial strand curls outward and the aecium is exposed. The presence of moisture causes the peridial strands to close. Simply breathing on the open aecia provides enough moisture to close them immediately. The alternate closing and opening of the aecium helps in the expulsion of the aeciospores.

The aeciospores are dark or nearly chocolate brown and, according to Pammel, (1905, p.18) vary from 26 to 33μ in diameter. Due to the pressure within the aecium, the developing aeciospores are polyhedral in shape. They possess thick cell walls. If they are mounted in a hanging drop of water, several light spots soon appear. These light spots evidently mark the location of the germ tubes which have yet to push outward. It is, however, very difficult to germinate aeciospores at this stage.

(b) Physiology

An histological study of the rust lesions has shown that

the substomal cavities of the infected portions of the leaf are obliterated. The spongy parenchyma is hypertrophied into closely packed columnar cells. The stomata seem to be uninjured but their functions are greatly affected.

The growth of rusted apple trees is certainly poor and the general vigor and physiological condition bad. Trees with a large amount of infection bear small apples with little market value.

The inability of the rusted apple leaves to regulate their transpiration is believed largely to account for this effect of the parasite upon the host. Transpiration of apple leaves infected with rust was investigated by Reed and Crabill (1915, p. 57) and the results compared with healthy leaves. The results showed:

(1) In daytime, the healthy leaves transpire more rapidly than the diseased.

(2) In darkness, the healthy leaves transpire less rapidly than the diseased.

(3) The transpiration of healthy leaves varies markedly with the light.

(4) The transpiration of diseased leaves is nearly constant whether they are in darkness or in daylight.

The conclusions drawn by Reed and Crabill to account for this situation were not definite. They felt that the stomates were affected in some way by the parasite, possibly by diffusible toxins, or that some other factor rendered them

immovable and unresponsive to light. Respiration in diseased leaves, however, was increased.

An attempt was made by Dr. W. B. Ellett, chemist of the Virginia Agricultural Experimental Station in 1911, 1912, and 1913 to determine whether there is any correlation between the activities of the leaves and the ash content. His results, published as a part of the work by Reed and Crabill in 1915, showed, on the average, that the ash content is uniformly greater in healthy leaves. No conclusions were drawn.

Analyses to determine the amounts of certain carbohydrates in healthy and diseased leaves were much more satisfactory. An examination of these results showed that the content of sugar, invert and total sugars, is higher in healthy leaves than in those affected with cedar rust. The material used was collected in August, 1913 and consisted of healthy and diseased leaves of York Imperial apples. The percent found in healthy as opposed to diseased leaves follows: (Reed and Crabill, 1915, p.57)

	Healthy	Diseased
Invert sugar	2.60	1.23
Total sugar	2.75	1.65
Starch	4.43	2.43

These results are in harmony with the determinations of the two classes of leaves as measured by the quantity of carbon dioxide used. In 1912, Reed, working with Cooley and Rogers, had found that carbon dioxide assimilation was greatly

retarded in rust infected apple leaves. It will also be noted that the amount of carbohydrate present in the diseased leaves was approximately 50 % of that in the healthy. This agreed with the carbon dioxide consumption of the two kinds of leaves as established by Reed and his fellow workers.

(1) Germination of Aeciospores

Heald, (1909, p.105) in making a careful study of the life history of the cedar rust fungus, observed that, "The first aecia become mature during the month of July and viable spores are produced in large numbers during this and the following two months."

Subsequent attempts by workers to germinate the aeciospores at this time met with conspicuous lack of success. Heald felt that it was during July, August and September that the infection took place. He noted, however, that the infection was not apparent during the remainder of the season and the winter season. Since the production of the cedar gall is dependent upon the growth of the cedar which is slightly or entirely inhibited at this period, Heald reasoned that the mycelium must remain dormant until the next spring. It was shown by Heald at this time that the aeciospores begin to lose their vitality during the months of September and October. Germination tests conducted on October 12, 1908 by Heald (1909, p.12) showed that only five percent of the spores examined were capable of germinating at a temperature of 26-28°C. while

only 2.4 percent germinated at field temperature.

Reed and Crabill, (1915, p.49) checking Heald's results, found too, that there was very poor germination of the aeciospore dispersal in 1912, 1913, and 1914. The results disclosed that sixty percent of the tests were entirely negative, i.e., there was no germination at all. The media used for these tests were distilled water in five instances and apple leaf juice. Four tests with water were made during the month of July, 1913 and one test during the middle of September, 1914. The test using apple leaf juice as a medium was made during August, 1912. Twelve percent germination was secured with an hanging drop of distilled water on August 13, 1912. Later, three percent germination was obtained by the same method on July 15, 1913. In two cases, water and cedar leaf juice yielded 3 and 0.5 percent germination respectively. Those aeciospores which did germinate put out a simple filamentous, vacuolate germ tube which grew to "some" length. In many cases, the ends of the germ tubes bulged out into simple enlargements, possibly indicating a feeble attempt to produce a secondary spore. The inability of the aeciospores to germinate under what seemed optimum conditions for spore germination threw some light on the time of infection of the cedar by the aeciospores.

At this point, Reed and Crabill felt that a more logical explanation than that offered by Heald was simply that aeciospores must undergo a resting period or exposure to winter conditions before they will germinate. The spores are distributed during the late summer and autumn, remain in the axils of

the cedar leaves where they have lodged and germinate the following spring. The young galls which result show up before any aecia of the current year's production are open. The view established that the mycelium is strictly annual and not perennial as Heald had pointed out.

Weimer (1917, p.517) two years later admitted that it was difficult to secure germination of the aeciospores immediately after dispersal. He felt, however, that the mycelium probably developed within the tissue of the cedar for a period of several months after infection occurred before any material change was noticeable.

However, Thomas and Mills (1929, p.29) substantiated Reed and Crabill's views through a series of germination tests. They felt that exposure to low temperature might increase the percentage of germination of the spores. Accordingly, aeciospores, after exposure to a temperature of 3°C were mounted in raised drops of distilled water at room temperature on December 6, 1928. A considerable number of the spores germinated. More extensive tests were made which made more conclusive the over-wintering theory. Germination results secured by Thomas and Mills after exposure of the spores to low temperatures were much higher than any recorded in the literature prior to 1929.

The germ tubes produced by this method were vigorous and reached lengths of 400 to 600μ in 24 hours even at 9°C. The results of their germination tests follow:

Temperature at which examined	Number examined	Percent of Germination
21°C	800	80.5
15°C	800	79.6
12°C	400	74.7
9°C	900	63.5
6°C	300	21.3

"The germination of fungus spores is difficult unless conditions favorable to their development are provided. Some conditions affecting germination include: maturity, longevity, temperature, moisture, light, oxygen, carbon dioxide, nutrients, pH, volatile substances, staling products and competition." (Riker and Riker, 1936, p.53)

C. Development of Epidemics

1. Correlation of Contributing Factors

The first requirement for the appearance of rust in an apple orchard is that infected cedars must be growing nearby. The density of the rust infection depends on three factors: the first, the relative positions of the two hosts; the second, the prevailing meteorological conditions during critical periods; and the third, the correlating development of apple foliage and dissemination of the sporidia.

Thaxter (1891) maintained that infection occurs if diseased cedar trees are eight miles distant, but it is generally accepted that an area of one mile radius free of

cedars around an orchard affords adequate commercial protection. Windbreaks of cedar trees planted close to orchards contribute to widespread infection because of the nearness of the two hosts. Prevailing winds easily carry the sporidia into the orchard.

In 1912, a striking difference was noted between the severity of cedar rust infection on trees bearing a light crop of fruit and those bearing a heavy crop. The latter were considerably less affected than those having little or no fruit. This was not an isolated case but one which caused much conjecture among orchardists. At present, there is no satisfactory explanation of this curious condition. It is difficult to determine what possible differences there might be between the foliage of a fruitful tree and that of an unproductive tree at the time infection is taking place, however great the physical and chemical differences might be later in the season.

2. Limiting Factors

Occasionally, the dissemination of sporidia may take place before the foliage of the apple trees has developed sufficiently to become infected and, on the other hand, it may take place after the foliage has become too old to be diseased. A majority of the observers, including Heald and Reed and Crabill, maintain that sporidia live for only a few days and unless conditions are exactly right, they come to naught. Hamilton, working in the Hudson Valley area in 1936, believes, on the

contrary, that the basidiospores remain viable for days or weeks. If that be true, it nullifies the formers' premises. However, Reed and Crabill performed definitive experiments to maintain their arguments.

NUMBER AND DISTRIBUTION OF CEDAR RUST INFECTIONS ON UNSPRAYED YORK IMPERIAL APPLE TREE. McDONALD ORCHARD - 1911.

	NUMBER OF CEDAR RUST INFECTIONS UPON LEAVES																			
	LEAF NUMBERS																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	TOTAL
TWIG I	1	0	0	0	0	0	0	0	0	0	0	0	13	34	30	16	30	7	0	131
TWIG II	0	0	0	0	0	0	0	0	0	20	12	28	42	11	1	0	0	0	0	114
TWIG III	0	0	0	0	0	0	0	0	1	5	17	36	24	28	3	0	0	0	0	114
TWIG IV	0	0	0	0	0	0	0	1	1	15	13	34	6	0	0	0	0	0	0	70
TWIG V	1	0	0	0	0	0	0	0	0	1	29	20	4	26	16	0	0	0	0	97
TWIG VI	1	0	0	0	0	0	0	0	1	23	39	40	22	14	0	0	0	0	0	140
TOTAL	3	0	0	0	0	0	0	1	3	64	110	158	111	113	50	16	30	7	0	666

The figures above show very strikingly the fact that apple leaves are only susceptible to infection with cedar rust during their early stages. The first nine leaves on these twigs are shown to have only seven of the 666 infections produced by the fungus. By the time the maximum infection was taking place, these early leaves were beyond the susceptible period and escaped infections. Penetration of the germ tubes takes place through the dorsal epidermis of the leaf and, therefore, it seems likely that the increasing thickness of cell walls and cuticle is the factor which determines the period of possible infection.

The season of 1911 afforded an almost ideal opportunity for making the above observations. The trees of the York Imperial put forth very few leaves until the blooming period is over. In 1911, the tree in question bloomed May 8th through May 13th. No rain of sufficient magnitude to produce sporidia occurred from the time that the leaves appeared until the evening of May 31st. The first nine leaves that developed on the apple tree passed the susceptible stage before any sporidia had access to them. The sudden increase in the amount of infection when the tenth leaf is reached is due to the fact that the rainfall on May 31st caused the cedar apples to put forth an abundance of gelatinous tendrils on which a large crop of sporidia were produced on the ensuing day. These sporidia infected the five or six leaves which had been unfolded just prior to June 1st. Another rainless period followed and the leaves that subsequently unfolded remained uninfected as

shown by the above data.

The conclusion was reached that the chief factor determining the amount of infection of susceptible leaves is the amount of moisture present and that this is necessarily modified by the numbers of sporidia coming from the red cedar tree.

In summing up the factors limiting the amount and distribution of basidiospore inoculum, one would list this multiplicity of factors: wetting periods, the relative situation of the cedars to the apples, the infestation of galls on the cedars, wind direction and velocity, presence or absence of intervening barriers such as woods, topography and elevation.

3. Critical Periods

Whether or not infection takes place depends in large part on the susceptibility of the host at the given time. The period of susceptibility is longer with the more susceptible apple varieties. The coincidence of a time of great sporidial dispersal with a time when a number of the leaves are young and not yet heavily cutinized or the fruit is immature will give maximum infection.

Giddings and Berg (Heald, 1933, p.808) state that: "A rain lasting at least two or three hours is usually required to bring about spore production and discharge on cedar apples; the rust spores are usually discharged for only a few hours

after a rain or between showers when the humidity of the air drops somewhat; the cedar apples are particularly active in discharging spores after a prolonged dry spell, but they appear to be temporarily exhausted after two or three closely successive periods of discharge; and ordinarily a wind velocity of three to four miles per hour is necessary for a sufficient distribution of spores to cause any general infection."

IV Control Measures

To avoid shortages and fluctuations in the apple crop annually, it is necessary to control cedar rust by spraying, dusting, eradication and planting resistant species.

A. Spraying and Dusting

One of the most generally accepted methods for controlling cedar rust is through the application of sprays or dusts. Numerous apple spraying experiments are reported in the literature on the subject and the results are varied as will be noted in the following observations.

Professor Galloway of the United States Department of Agriculture (1889, p.413) gave data on spraying experiments for apple rust control at Vineland, New Jersey. With reference to an experiment with Bordeaux mixture, he stated that the foliage remained fairly healthy yet the benefit was not sufficient return for the labor expended.

Professor L. R. Jones (1891, p.139) conducted an experiment in the orchard of Mr. John E. Smith in South Burlington, Vermont in 1889. On May 17th and May 30th, he sprayed the trees with ammoniacal copper carbonate. The following proportions were used: One ounce copper carbonate distilled in one quart of ammonia first distilled in twenty-five gallons of water. The May 30th spray solution was diluted by adding one-half more

water than previously. The results showed no outstanding difference in the percent of rusted leaves, (75% of the sprayed leaves were rusted as against 77% of the leaves on control trees) but the number of rust spots per rusted leaf was less on the sprayed than the unsprayed trees. The true benefit of the spraying was greater than the above figures indicate because previously, the sprayed trees had been infected considerably more than the other.

Pammel (p.43) at about the same time reported spraying wild crab apple trees with three applications; two of Bordeaux mixture and the last with ammonical carbonate of copper. He worked in Iowa where the disease was not yet prevalent. He concluded there was little benefit from spraying.

In 1892, Jones again reported on spraying experiments. He secured fair results but did not feel that this method of control was very practical.

Austin (1901, p.296) pursued the following spray schedule: Trees were carefully sprayed March 24th before growth started, April 25th, May 4th, May 22nd, June 5th, June 20th, July 23rd, August 9th and August 28th. The trees were examined on October 10th and it was found they were as badly infected as they had been the previous year with no sprayings.

Professor Emerson reported in the Iowa Homestead (1905, p.669) that he sprayed twenty-two Wealthy and eight Jonathan trees with from one to three applications of Bordeaux. The dates of spraying were April 26th, April 27th, May 7th, May 9th, May 23rd and May 28th. Trees that were sprayed on May 7th or

May 9th showed remarkable control. He concluded that spraying at the crucial moment when cedar apples are in a germinating condition gives excellent results and the time of spraying must vary with the season.

In 1908, Hein remarked that it was sometimes recommended that apple trees be sprayed with Bordeaux mixture or other fungicide to prevent rust but his experience of three years of spraying showed notably few beneficial results.

Heald in the same year decided to attack the problem from another angle. He proposed spraying the cedars to prevent the development of cedar apples. Using 6-6-48 Bordeaux plus three pounds of soap on July 26th, August 6th and August 15th, he sprayed one tree. This cedar had 48 galls as compared to 950 on the control tree. This was encouraging, but unfortunately he found that the reduced number of galls bore no direct relation to the infections of neighboring apple trees. They were as badly infected as others. However, it did prove a good method to save any valuable cedar whose life was being threatened by the fungus.

Stewart (1910, p.316) reported that a Mr. F. A. Serrine had sprayed his Long Island orchard for several years with Bordeaux mixture with little success. However, in 1909, trees given two sprayings of 3-3-50 Bordeaux showed only 10% as much infection as unsprayed trees.

In 1913, Giddings (p.3) reported a case in which one application of spray controlled the rust well.

Reed, Cooley and Rogers (1912, p.7) said they had tried

various and sundry spray materials and none had proved too effective.

Bartholomew (1912, p.253) applied Bordeaux mixture on May 15th, May 22nd and May 30th. He remarked that the spraying was done "immediately following the formation on the cedar galls of the jelly-like telial extrusions" and "before sufficient time had elapsed for the transfer of the sporidia from the galls to the apple foliage." The trees thus sprayed showed a marked decrease in the percentage of infected leaves. Agreeing with Professor Emerson (see above) he concluded that; "The proper time of spraying cannot be designated by any fixed dates for the crucial time for action depends entirely upon such weather conditions as favor the development of the cedar galls."

Giddings and Neal (1913, p.258) found it possible to control apple rust by using sprays of lime sulphur, Bordeaux mixture or atomic sulphur.

Reed, Cooley and Crabill found a copper-lime-sulphur spray especially effective in 1914.

Working in West Virginia with dusts, Giddings and Berg rated 1-40 lime sulphur best, Bordeaux mixture second and atomic sulphur third. Dusting has not proved to be a reliable practice, however.

Reed and Crabill in 1915 (p.16) reported briefly on the results of the toxic action of some sprays upon the viability of the teliospores. They found Bordeaux mixture, copper-lime-sulphur and iron Bordeaux all successfully inhibited germination. Lime sulphur proved unsuccessful. They

experimented more extensively with the effect of spray materials on sporidial germination. Here, Bordeaux mixture, Pyrox, lime sulphur, copper-lime-sulphur and Sulfocide all had strong toxic action. They stated, "The results of our work indicate that spraying is generally effective in controlling the cedar rust provided the applications can be made at the right time. If young apple leaves can be coated with spray mixture soon after they unfold and kept coated until the first week in June, spraying will be effective in preventing infection. In the case of the York Imperial, it is unnecessary to spray until the trees have blossomed although the spraying may well be done when a few petals still cling to the trees. In case of varieties like Jonathan and Arkansas Black, which put forth their foliage in advance of the blossoms, it may be necessary to spray before the blossoms appear. Subsequent applications of spray materials should be made often enough to protect new leaves as they appear."

The greatest efficiency in preventing infection is obtained when the spray material is applied just previous to rainfall or as soon thereafter as possible. A delay of one day may allow so much infection as to render the spray ineffective.

The spray materials found to have the greatest efficiency were Bordeaux mixture, iron Bordeaux, lime sulphur and copper-lime-sulphur. Other things being equal, the more adhesive materials are the more efficient.

Spray injury was observed on trees sprayed with materials containing copper if rainy weather of several days duration

followed the applications. Since the time in which spraying may be done is so limited, it is generally impractical to spray all the trees in a large orchard at one time, and it is more economical to destroy the neighboring cedar trees.

Fromme and Thomas (1917, p.179) reported on the ineffectiveness of a fixed spray schedule as commonly used in the cedar infested regions of Virginia. To be useful, applications should be made before sporidial dispersal, i.e., following rains of at least four to six hours in the normal discharge period between April 15 to June 1st. If such rains could be predicted early enough to allow the orchardist to spray susceptible trees, cedar rust could be effectively controlled. This is obviously impractical in cedar-ridden Virginia where control work of necessity is a matter of cedar eradication.

These men reasoned that perhaps dusting, with its speedier application methods and its light equipment might permit larger areas to be treated more quickly and efficiently. They tried it in 1916 but it was a complete failure. The only reason they could advance for this was that the dust probably did not go into solution rapidly enough to stop germination and infection.

From 1917 to 1934 little progress was made on the problem of fungicidal control. In 1934, Crowell reported the first definite advance in this field. During a careful series of experiments conducted at the Arnold Arboretum in Massachusetts, Crowell tested sixteen spray combinations at various concentrations and recorded excellent results on the most susceptible

apple trees by using $\frac{1}{2}$% Linco Colloidal Sulphur as a protective spray against infection by the fungus. The material used has been found to be effective over much longer periods of time than previous sprays. It was, therefore, possible to devise the following spray schedule which would prevent infection by the rust fungus as well as apple scab:

"<u>First spray</u>: Before the first expected rains after the buds have opened. In Massachusetts, about May 1st. This spray may coincide with the second.

<u>Second spray</u>: The so-called 'pink spray', after the cluster buds have separated but before the petals have expanded.

<u>Third Spray</u>: The so-called 'calyx spray'. When the petals are two-thirds off.

<u>Fourth Spray</u>: Ten to fourteen days later. Shorter intervals if weather is rainy. Linco Colloidal Sulphur will remain effective after two or three moderate rains.

<u>Fifth Spray</u>: Ten to fourteen days after fourth providing telia are still present on cedar trees."

The possibilities of a sound and practical control program have been greatly enhanced since 1934. Crowell's work was a great step forward and left little to be desired. The years will probably force some modifications upon the above schedule but the orchardist, at last, is confident that he has the knowledge and materials to combat cedar rust infection.

B. Eradication

Although Jones is credited with being the first to recommend the control of cedar rust through eradication of the cedar trees, an examination of the literature reveals that Thaxter two years before was aware of such control measures. In a paper published in 1891 (p.3), Thaxter stated that certain rusts on apples may be controlled by "cutting down adjacent cedars as far as it is practicable; for although it has been shown that infection from cedars may take place at a distance of eight miles, the virulence of the disease is of course proportionate to the proximity of the cedars."

The findings of Jones and Thaxter have been repeatedly confirmed and the interruption of the life cycle of the pathogene through the destruction of the cedar has since been widely practiced.

In 1905, Pammel called attention to the danger of the common use of the red cedar as a windbreak or for ornamental planting when the cedars were in close proximity to fruit trees.

In spite of the apparent value of this method of control, it proved difficult to convince skeptical farmers of its worth. Some farmers valued the cedars more than they valued their few apple trees. Much potential infection material was, therefore, maintained as a constant threat to nearby commercial orchards. The farmers who did become convinced that the cedar tree was responsible for one stage in the propagation of this disease found that their orchards were surprisingly benefited when the

cedars were removed. Various state plant pathology departments began about 1910 to advise that cut cedar trees be burned because it was shown that the cedar galls were capable of producing sporidia for about two months after the trees were cut down.

Reed, Cooley and Crabill recommended a cedar-free area of one-half mile around apple orchards in Virginia in 1914.

Giddings and Berg (1915) in West Virginia, Jones and Bartholomew (1915) in Wisconsin, Stewart (1920) in New York and Talbert (1925) in Missouri strongly advocated the removal of the red cedars as the most certain and most practical means of combating cedar rust within their respective states.

The Cedar Rust Law which was enacted in Virginia in 1914 brought excellent results although many bitter objections were made by cedar owners. The law was gradually amended so that cedar eradication became optional in certain cases. At the present time, the law has questionable value.

Crowell (1934, p.203) lists eleven states in the eastern part of the country which have either a cedar eradication law or a plant pest law. Most of these states no longer enforce cedar eradication, however.

While field workers generally recognize the practicality of eradication as a control measure, the emphasis seems to be shifting to the use of sprays and the planting of resistant varieties.

Heald (1933, p.803) summarizes the control measures which affect the cedar as follows:

(1) "Remove and destroy all cedar trees within a radius of one mile around the apple orchard.

(2) "Avoid the use of cedars for windbreaks around orchards or for ornamental plantings within a mile of apple orchards.

(3) "In the case of a few small isolated cedars, the removal of the galls previous to the production of the gelatinous sori will afford protection.

(4) "Avoid planting the <u>Juniperus virginiana</u>, <u>Juniperus virginiana</u>, var. <u>Scottei</u>, <u>Juniperus virginiana</u> var. <u>glauca</u> and <u>Juniperus sabina</u> var. <u>fastigiata</u> as the fungus has been found on all these forms."

In the case of a few isolated or wild apple trees near prized cedars, the life cycle may be broken by cutting down the apple trees. It is for the worker to decide whether he will control the disease through spraying which is effective under certain conditions, through eradication which is permanent or through the selection and planting of resistant varieties.

C. Resistant Varieties

Studies on the varietal susceptibility of various types of apples has focused much attention on the value of planting resistant varieties as a contol measure. Workers in the field early found that some trees were little affected by the fungus. Later workers through controlled inoculation experiments extended the known lists of resistant varieties. There is, however, some lack of complete agreement on the part of workers

as to what varieties are immune or resistant to the disease. Jones and Bartholomew (1915) cautioned that observations have been too limited for broad conclusions, especially when one remembers that disease resistance is a relative character which may change with environmental changes. The Ben Davis, as an example, has been listed as susceptible in Virginia, moderately susceptible in West Virginia and resistant in Nebraska.

Pammel in 1905 listed the following as more or less resistant:

Oldenburg	Fameuse
Hibernal	Canada Baldwin

Listed by Pammel (1905) as resistant in Iowa were:

Cooper's Early	Ben Davis
Early Harvest	Gano
Sweet June	Winesap
Yellow Transparent	Mammoth Black Twig
Red Astrachan	Ralle's Genet
Maiden Blush	Northwest Greening
York Imperial	Grimes Golden

The following is a composite list of resistant varieties as reported from several different states: Nebraska by Hein in 1908; Virginia by Reed, Cooley and Crabill in 1914; West Virginia by Giddings and Berg in 1915; Iowa by Pammel in 1905; and Connecticut by Clinton and Britton in 1911:

Baldwin	Wolf River
Maiden Blush	Yellow Transparent
McIntosh	

These were all uniformly listed as resistant. Reports indicate that the Ben Davis, York Imperial and Maiden Blush are not listed as resistant in all sections.

One of the dangers, therefore, to the planting of resistant apple varieties lies in the lack of agreement among workers on what constitutes immunity or resistance. The fact remains that apples vary in their susceptibility not only to different species but also to different strains of the rust fungi.

Farmers having established orchards of rust susceptible varieties cannot always afford to remove them and replant with rust resistant varieties.

Efforts to develop disease resistant varieties have been receiving greater and greater attention. The field of plant breeding through selection and induced variation of resistant varieties is still before us and may shortly open a whole new approach to the complex problem of control.

Summary

Specific statements of work completed and progress made to date are given along with some mention of the need for further investigations on certain aspects of the subject which offer most favorable opportunities for further study. Among these are:

(1) The need for scientific knowledge concerning the conditions affecting germination of the aeciospores. At the present time, it is not understood if germination of the aeciospores begins immediately or they overwinter on the cedar. Freshly diseased material should be studied for the location of mycelium and its effect on the host tissue.

(2) The necessity to investigate further into the factors opposing the entrance of the parasite into the host.

(3) The need to field test the spray schedule devised by Dr. Ivan Crowell in other states and with apple varieties with varying blooming periods.

(4) Further investigation should be made to expand the known list of alternate hosts.

(5) Education is needed to discourage the planting of red cedars in the vicinity of established orchards of a susceptible variety.

(6) The problem of control on the cedar tree has been unsuccessful to date. This has been due to the fact that while the germination of exposed teliospores

may be controlled, further protrusion of telial material produced additional fertile spores.

(7) The great differences recorded by various workers with varietal susceptibility indicates the need for further work to account for this lack of uniformity.

Considerable difficulty was experienced with certain writers who drew conclusions but neglected to state all the factors which were influential in causing these decisions.

A great deal of the early observations made on cedar apple rust were under conditions that were not controlled by the investigator. The trend is toward the observation of phenomena under rigidly controlled conditions.

In a few cases, investigators proposed hypotheses but did not attempt to determine the validity of the hypotheses. For example, in the section on control, it will be noted that very little progress was made from 1914 to 1934 because many workers failed to recognize the causal connection between things and events. One writer mentioned that a single spray seemed to control the rust in a given year. No attempt was made to show that the results were determined by certain operative conditions and occur only when these conditions are present. In very few original papers were meteorological records included to show which factors were operative at any given time. This made it difficult for the reader to build a working hypothesis upon which further observations could be made.

The progress in this field has brought about the saving of many thousands of dollars through education of the orchardist to an awareness of the situation. Disastrous fluctuations of yield have become less common and higher quality of products has resulted from an application of knowledge now available.

ABSTRACT

In this paper, certain general considerations are given pertaining to the history of the disease known most commonly as cedar apple rust.

The fungus is shown to be heteroecious, i.e., it requires two host plants for its complete development. The red cedar serves as a host during the development of the telial and sporidial stages, the pomaceous tree during the spermatial and aecial stages.

Cedar rust is found to be one of the true rust fungi, Gymnosporangium juniperi-virginianae Schw. It is necessary for the perpetuation of the disease that the two hosts be near each other.

The life cycle of the disease is discussed with some comment concerning factors influencing spore dispersal. The study includes:

(1) the entrance of the pathogene into the pomaceous host
(2) its establishment and development in the host
(3) its exit from infected regions of the host
(4) its dispersal to the red cedar

The symptoms of cedar apple rust on both the cedar and susceptible apple varieties are dealt with at length.

The geographical range of the disease has been plotted through reports contributed by field workers.

Plant pathologists are not agreed on the economic importance of apple rust. The disease has become severe enough to necessitate preventive measures only comparatively recently. The potential reduction of marketable apples and the reduced vitality of the trees probably constitute the major dangers of cedar rust infection.

The taxonomy of <u>Gymnosporangium juniperi-virginianae</u> is summarized.

The morphology of the normal cedar leaf is considered briefly in order to understand the nature of the infective process and the formation of the gall. The abnormal gall tissues are contrasted with normal tissues.

Some suggestions relating to the methods and procedures for determining spore frequency in the air are discussed as are investigations pertaining to the factors which influence sporidial production.

The technique of inoculations designed to bring the fungus to a susceptible or suspected host under conditions favorable for infection is reviewed from an historical point of view. The susceptibility of the host plant may be influenced by a number of factors including age, vigor, previous treatment, previous inoculation, moisture, subsequent treatment, environment during inoculation, morphological condition, physiological condition and temperature.

To a large extent, weather conditions have been found to govern the amount of rust in any specific season. The

germination of the teliospores and the infection of the aecial host require moisture and, therefore, the number of rain periods governs the number of infection periods.

Certain suggested reasons are noted to account for the lack of uniformity among workers concerning varietal susceptibility of apples. Lists showing degrees of resistance by apple varieties are included. There is some discussion of certain external and mechanical characters which oppose the entrance of the parasite into the host.

Emphasis has been placed upon the study of normal and diseased apple tissues. A comparison of the mycelium of the parasite in the pomaceous host and that found in the hypertrophied gall is made. The effect of the parasite on the leaf is developed from a morphological and physiological viewpoint. The transpiration of leaves infected with apple rust is compared with the transpiration of healthy leaves. An analysis of the amounts of certain carbohydrates in healthy and diseased leaves is given.

The problem of aeciospore germination, which caused great trouble to early workers, is developed.

There is an attempt made to show that the correlation of contributing factors results in the development of epidemics.

The multiplicity of factors which limit the amount and distribution of basidiospore inoculum is discussed and summarized.

Control measures designed to avoid shortages and

fluctuations in the apple crop form one of the major sections of the paper. Specific attention is devoted to control by spraying, dusting, eradication and the planting of resistant species.

A consideration of the historical background reveals that while important advances were made through the years, no adequate spray schedule was formulated until about 1935.

The possibility that the disease might be controlled on the cedar tree was considered but a survey of existing literature revealed that this method of control has been unsatisfactory.

The excellent results reported by Dr. Ivan Crowell with ½% Linco Colloidal Sulphur as a protective spray against infection by the fungus are duly recorded. Some notice is also given his promising fixed spray schedule. The orchardist at last is confident that he has the knowledge and materials to combat cedar rust infection.

A section is devoted to legislation which enabled the plant pathologist to use eradication as a control measure. The attempts to lessen the disease by legal eradication of the cedars were successful at first but are now little practiced because of numerous protests by cedar owners. The trend away from eradication and toward the use of resistant varieties and sprays is pronounced.

Lists of plants resistant to the disease are included, which are of aid primarily to the orchardist setting out a new group of trees.

A complete bibliography and several diagrams and tables are included.

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APPENDICES

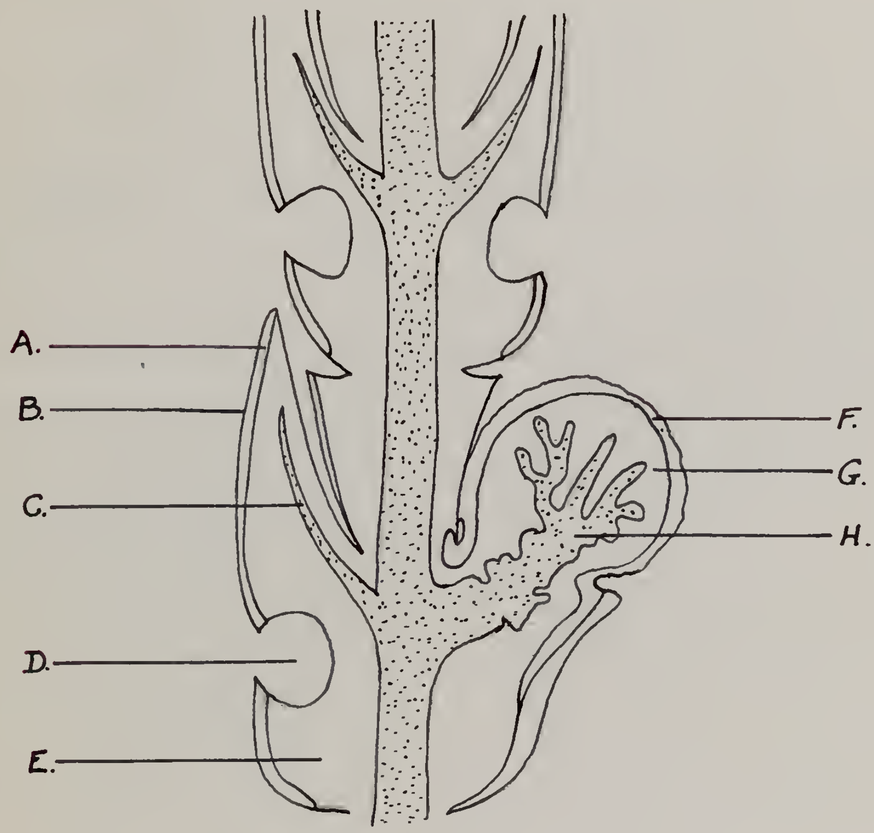
Diagram 1. Cedar Gall--Late Spring

The disease appears on the red cedar in the form of galls which increase gradually in size until they reach a diameter of nearly two inches. The color of the young gall is first green but it gradually becomes brown as maturity nears. The reniform, globular, or sub-globular surface of the gall shows rounded depressions at this time. The number of depressions is usually in direct relation to the size of the gall.

. CEDAR GALL - LATE SPRING (X2) .

Diagram 2. Minute Structure of Gall

DIAGRAM 2.– LONGITUDINAL SECTION OF A CEDAR TWIG BEARING A MINUTE CEDAR APPLE COLLECTED DURING THE MONTH OF JUNE



A. EPIDERMIS

B. SCLERENCHYMATOUS LAYER

C. FIBROVASCULAR BUNDLE

D. RESIN GLAND

E. PARENCHYMA

F. CORTEX

G. PARENCHYMA OF CEDAR APPLE

H. FIBRO-VASCULAR SYSTEM OF CEDAR APPLE

Diagram 3. Cedar Gall--Telia beginning to Emerge

In April or May, during the first warm spring rains, elongated, gelatinous, orange-colored horns or telia are projected forth at the site of the circular depressions. Galls at this stage are popularly known as "cedar flowers".

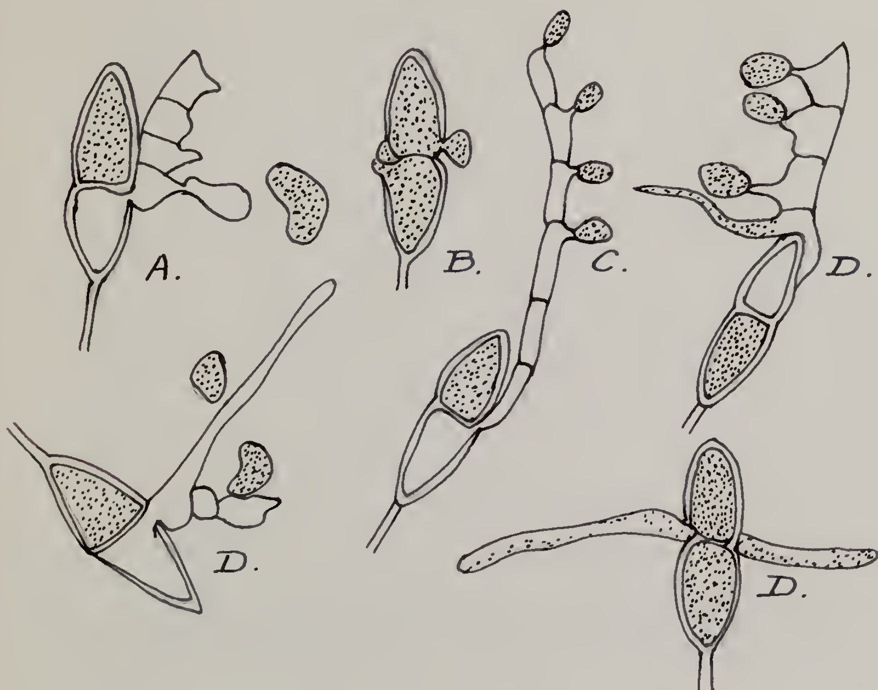
CEDAR GALL—TELIA BEGINNING TO EMERGE.
(X 2)

Diagram 4

Germination of Teliospores of

<u>Gymnosporangium juniperi-virginianae</u>

DIAGRAM 4. GERMINATION OF TELIOSPORES



AFTER HEALD.

A. TYPICAL GERMINATION - COMPACT FORM

B. TELIOSPORE SHOWING DIRECT PRODUCTION OF SPORIDIA

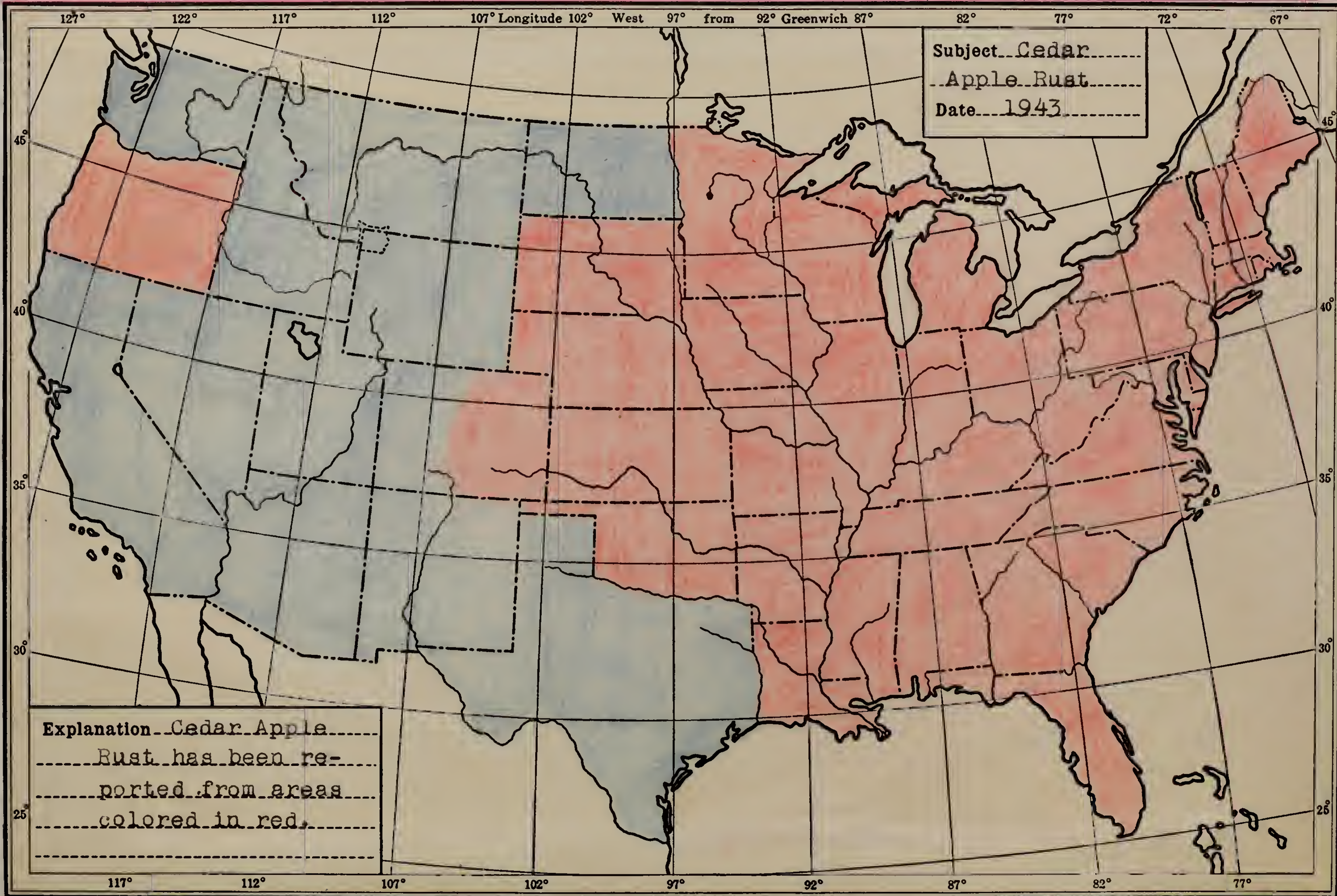
C. TYPICAL GERMINATION - ELONGATED FORM

D. PROMYCELIA SHOWING DEVIATIONS FROM THE TYPICAL

Map 1

Geographical Range of

Gymnosporangium juniperi-virginianae



Subject Cedar Apple Rust
Date 1943

Explanation Cedar Apple Rust has been reported from areas colored in red.